Dispatches

# Animal Eyes: Defending the Coat of Mail

**The eyes on the backs of molluscs known as chitons are shadow and motion detectors, the lenses of which are made of birefringent aragonite. These provide a focus both in and out of water.**

**Michael F. Land**

The eyes of vertebrates or insects serve many functions, supplying information about the form, location, motion and ultimately the identity of objects in the surroundings. Multi-purpose visual computation on this scale is neurally expensive, and in visually advanced animals it is typical for up to half the brain to be devoted to visual processing [1]. At the other extreme there are visual systems that have only a single function. For a flatworm, for example, this may involve no more than finding a dark corner to lurk in during the day, and this needs very little sophistication of either eye or brain. One task, however, does require a reasonably well-resolved image, although not necessarily much brain power. This is predator detection. Predators make their presence known visually by their movements, and so an organism can protect itself by having some kind of motion detector linked to a defensive response — such as closing its shell, or sealing itself onto a rock — that will keep it out of harm's way.

Chitons, or coat-of-mail shells, are a very ancient branch of the molluscs characterised by having a shell made of eight separate plates. They are grazers, rasping algae from marine rocks, and they have a defence strategy based on shadow and movement detection. This was first described by Crozier and Arey in 1918 [2], who observed that even the shadow of a passing fly would halt a chiton's progress. In this issue of *Current Biology*, Speiser *et al.* [3] describe the unusual optical structures that make such responses possible, and measure their performance.

Most chitons have very small photoreceptor structures dotted across the surface of the shell plates. These are known, intriguingly, as 'aesthetes'; they have little or no optical structure, but they do respond to shadow. In two chiton lineages, however, there are larger structures which are referred to as ocelli, and in *Acanthopleura granulata* these are up to 80 μm across. They each have a lens and below this a cup of microvillous receptors. The structure of the lenses is unique: they are made of aragonite, a type of calcium carbonate that forms the rest of the chiton shell. Most other biological lenses are made of protein, chitin or, in the case of certain trilobites, calcite. Aragonite is birefringent, with refractive indices of 1.53 and 1.68, and this means that lenses made of aragonite can potentially have two focal lengths. Speiser *et al.* [3] point out that chitons operate both in and out of water, and they make a strong case for believing that each of the two focal lengths allows the lens to focus an image onto the retina in one or other medium.

This conclusion is reinforced by a test of *Acanthopleura*'s visual performance. It will respond, by withdrawing down to the substrate, when a 9° (or larger) black disc appears, or is moved, above it; however, it will not respond to the same amount of dimming when this is distributed across the whole field, demonstrating that the disc is indeed resolved. The 9° threshold also corresponds to the angle of view of one retinal receptor, and the same threshold is found whether the chiton is in air or water, which tends to confirm that an image is resolved in both media.

Amongst the grazing and filter-feeding molluscs and annelids there are many animals that have adopted the same strategy, and in the process have come up with a number of 'one-off ' eye designs of impressive diversity. Amongst the bivalves there are pin-hole eyes in giant clams [4], concave reflector eyes in scallops [5], and small compound eyes in ark clams [6] (Figure 1). These are all animals that need to avoid having their tentacles nibbled by passing fish. Similarly, in the sabellid tube worms, which have a fan of filter-feeding tentacles, there are small compound eyes on some of the tentacles, and when stimulated these provoke a swift retraction into the tube.

Figure 1. Shadow and movement detecting eyes in molluscs.

Top: lens eyes of the chiton *Acanthopleura*. Eye diameter 60 μm (Daniel Speiser). Middle: concave mirror eyes of the scallop *Pecten*. Diameter 1 mm (Michael Land). Bottom: compound eye of the arc clam *Barbatia*. Diameter 200 μm (Dan-Eric Nilsson).

Nilsson [6] has referred to eyes such as these as 'burglar alarms'. None of these eyes, including those of chitons, is a 'true' motion detector: that is, they do not compare sequential stimulation across the retina, as in insect or vertebrate eyes. Motion is detected simply as the dimming of one or more receptors, as the image of a dark object moves across the retinal array.

The photoreceptors involved in these unconventional eyes are interesting because they are usually different from those of the eyes borne on the head. Modern ideas about the evolution of photoreceptor types [7] indicate that the early bilaterians had two types of receptor: rhabdomeric receptors based on microvilli which depolarise to light, and ciliary receptors that hyperpolarise when illuminated and respond when darkened. In general the deuterostomes (incuding us and echinoderms) employ ciliary receptors and the protostomes (including molluscs, annelids and arthropods) employ rhabdomeric receptors in their main organs of sight.

In the molluscs, it seems that there are actually plenty of examples of both types of photoreceptor. Gastropod snails generally have a pair of cephalic eyes which direct locomotion. These are either simple pit eyes or have lenses of varying quality, and they invariably have microvillous on-responding receptors. The receptors that respond to shadow and cause withdrawal are not in the cephalic eyes, but located elsewhere on the body. The marine pulmonate slug *Onchidium verruculatum* has two types of eye: conventional cephalic eyes, and about 30 quite different eyes on papillae on its back. The latter have ciliary receptors and respond to shadow and probably movement [8]. The mantle eyes of bivalves are unlike cephalic eyes in optical structure (they tend not to have conventional lens optics), and in function, location and origin. They also typically have ciliary receptors that give off responses — although the opsins involved are not identical to the vertebrate opsins [7]. Chitons, which are only distant relatives of gastropods and bivalves, have no head and no cephalic eyes. The receptors in the dorsal ocelli seem to go against the general trend in that they are rhabdomeric [9], yet mediate shadow responses. This apparent anomaly might be worth another look.

The eyes of modern vertebrates, cephalopods and arthropods, backed up by impressive processing power, must all have originated in organs with a limited range of functions. Did they begin as devices for detecting prey, or predators, or mates, or for finding the right habitat, or for simply not bumping into things? Can the range of still-existing eyes with limited functions tell us much about the route or routes to visual multi-competence that must have occurred several times during the Cambrian and shortly thereafter? My guess is that the molluscan predator detectors were not on that route, but we still have few clues as to what was.

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# Developmental Biology: Small RNAs Play Their Part

**What mechanisms coordinate the sequential pattern of gene expression during development of specialized cells? A small RNA-based mechanism is proposed to repress expression of genes during oogenesis.**

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Development of specialized cells typically requires the coordinated expression of genes as cells progress through developmental stages. During oocyte formation, coordinated gene expression allows germ cells to move through the stages of oogenesis and generate the numerous mRNAs and proteins that are stored in the oocyte for later use in the embryo. Various regulatory mechanisms have been implicated in the timely activation and repression of gene expression during germline development. In a recent issue of *Current Biology*, Maniar and Fire [1] provide an intriguing hypothesis for how small RNAs may participate in the coordinated repression of gene expression during *Caenorhabditis elegans* oogenesis.

Many components of the small RNA machinery promote development in plants, fungi, and animals, and it is becoming clear that small RNAs regulate developmental gene expression. In many organisms, RNA-dependent RNA polymerases (RdRPs) generate small RNAs during both RNA interference and normal development [2–8], and mutations in many RdRPs cause developmental defects (e.g., [5,9–15]). Unlike microRNAs, which are encoded by the genome, small RNAs have been particularly challenging to study because they are produced from RNA templates; consequently, it has not been possible to mutate specific small RNAs without also mutating the original, transcribed gene. Nonetheless, an appealing hypothesis, given the pleiotropic RdRP mutant phenotypes and the prevalence of endogenous small RNA sequences, is that these factors participate in mechanisms to limit the expression